directly to the upper steady state. S phase will be initiated as CDK activity crosses the lower threshold (red bar), but whether or not the cell is able to complete the replication of its DNA before it crosses the upper threshold (blue bar) and enters mitosis depends on how fast the fusion protein is accumulating in the mutant cell. In a wild-type genetic background, the Cdc13–Cdc2AF heterodimer accumulates very quickly, and these cells enter mitosis with incompletely replicated DNA, causing a mitotic catastrophe. But the fusion protein apparently accumulates more slowly, giving most cells enough time to finish DNA replication before the sister chromatids are pulled apart at anaphase.

In summary, the cell cycle crank can be turned, in principle, by a single cyclin-dependent protein kinase whose activity fluctuates between sufficiently low and high values, due to the influences of regulatory proteins. The dynamical system creates a series of switch-like transitions that guarantee irreversible progression through the classical phases of the eukaryotic cell cycle.

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Structural Colour: Elusive Iridescence Strategies Brought to Light

Understanding structural colours in nature requires the right set of optical experiments: this is illustrated by a new study on iridescent bird of paradise feathers, which suggests the potential behavioural importance of dynamic colour changes.

Pete Vukusic

The colours of many animals and some plants are brought about by an interaction of incident light with periodic nanostructure. Such effects are referred to as structural colours [1,2] and they offer distinct advantages over pigment-based colour generation for the control of hue, brightness, saturation, directionality and polarisation [2,3]. There has been keen interdisciplinary interest in understanding this aspect of biological systems, in part because of the emergence of photonics as a technological field since the 1990s [4] but also for the insight it offers students of animal behaviour.

The performance and function of such simpler systems as biological multilayers are well recognized [2], but despite recent progress in the use and development of measurement and modeling techniques in this area, there are many other structurally coloured systems whose detailed action and function are poorly understood. This is largely due to the morphological complexity of their systems' inherent photonic structures, which makes it difficult to discern their role and effectiveness. Photonic effects arising from complex system designs are usually attributed generically to coherent scattering and their purpose ascribed generally to conspecific communication or to camouflage. This is rather too vague, however, and it invariably overlooks strategic design features that have key implications in aspects of display behaviour.

Several factors may contribute to the complexity of a system. For instance, it may involve more than one photonic subsystem of dissimilarly dimensioned refractive index periodicities (for example, some structurally coloured butterfly scales exhibit both one-dimensional and three-dimensional periodic structures [5]). It may also comprise strongly narrowband or broadband absorbing pigment that is diffusely or discretely located within or without an inherent photonic substructure. And there may be significant variations about a mean value of refractive index periodicity, a biological noise of sorts, which supplements or complements the sample's inherent structural order or quasi-order. Furthermore, such periodicity may itself be formed within an overall geometric envelope that considerably influences its far-field optical signature. Achieving a fundamental grasp of any resulting

light-manipulation mechanisms is no easy task. It is clear that, in many cases, the key obstacle to understanding systems' action and function is an inability to collect sufficiently detailed and informative experimental optical data. While standard spectrometry and electron microscopy can provide adequate information for the examination of simpler systems, in many other species it does not provide the necessary revelatory evidence on which precise explanations can be based.

For the experimental optical investigation of structurally coloured biological systems that serve an optical or an appearance-related function, certain key questions should be asked. For instance, what are the angle-dependent, wavelength-dependent, and polarization-dependent properties of the system's reflectance (R_θ, R_λ and R_{pol}, respectively)? Furthermore, and often more importantly for biological systems in terms of their implication for behavioural signaling, what is the far-field spatial distribution of R_θ, R_λ and R_{pol} — a property called the bidirectional reflectance distribution function (BRDF) [6]? Without unambiguous answers to these questions the underlying purpose and utility for such complex photonic designs can be unclear.

Instruments for accurate quantified measurement of a sample's BRDF have existed for some time [7,8]. But it is only recently that such an instrument has purposely been designed for and applied to the study of structurally coloured biological samples [9]. A new study by Stavenga *et al.* [10] illustrates the elegant and effective use of this instrument in an optical investigation of the iridescent plumage of male Lawes' Parotia (*Parotia lawesii* Ramsay, 1885; Aves: Paradisaeidae). This bird species is well-known for its ultra-bright and rapidly-changing saturated iridescent chest-feather colours that take centre-stage during courtship display [11,12].

Structurally coloured birds' feathers tend to comprise ordered or quasi-ordered variations in refractive index through one or other of two designs: by the presence of spatially-arranged melanin cylinders embedded in a surrounding medium of keratin; or by the presence of air spaces in a spongy keratin matrix [13]. In *P. lawesii* feather barbules, arrays of spatially ordered melanin cylinders are situated in a keratin medium. However, the geometry of the barbule cross-section is intriguingly curved: Stavenga *et al.* [10] refer to it as a *boomerang* shape. This feather barbule shape was previously identified by electron microscopy and reported [14,15], but a light and colour manipulation effect was not attributed to it beyond basic interference in the melanin-keratin periodicity. The far-field behaviour of this boomerang-shaped multilayer remained uncharacterised and its consequent effect on the feathers' appearance remained unexplained, its potential contribution to display behavior unclear.

Stavenga *et al.* [10] collected detailed BRDF data from the breast-plate feather barbules and used them, alongside high-quality optical microspectrometry and transmission electron microscopy (TEM) images of the barbules' cross-sections, to explain the underlying optical processes. Importantly, the BRDF data, namely the spatial distribution of R_λ and R_θ, confirmed that the multilayer geometry imposed by the uniquely curved cross-sectional shape of this species' barbules enables it to reflect intense saturated colour concurrently in three different directions. Furthermore, access to the barbules' BRDF enabled detailed quantification of the unusually abrupt and dramatic change in feather hue with changes in the angle of observation of the barbules (as the courting male re-orients himself in front of the female). This is an optical effect which a human observer notices but which until now has been unquantified and its mechanism poorly understood.

Rapid and intense changes in animals' structural colours, whether through dynamic [16] or orientational [17] means, require structures or processes that are costly to create. Such are the costs and, invariably, such is the optical efficiency and the optimisation of the systems' designs, that significant biological function should genuinely be served [18]. It is intriguing to consider the degree to which the rapidity and extent of structural colour change in a displaying animal is intrinsic to its signaling. Stavenga *et al.* [10] maintain that the *P. lawesii* feather barbule design appears very highly adapted for the purpose of promoting during display stronger and faster hue shifts when compared to most other iridescent feather systems. Although no behavioural data yet exist to indicate the response of birds such as this to dynamic chromatic variations, the BRDF data the authors have collected, and the resulting explanation they present, strongly support this contention.

Control not just of colour reflection but of the directional distribution of colour reflectance is likely to be a key behaviourally-linked characteristic of many iridescent animals and plants. From an optical measurement perspective, the detailed quantification of all three of the variables R_θ, R_λ and R_{pol}, and specifically of the BRDF, will bring about a more complete understanding of the mechanisms that underpin the performance of complex samples' photonic designs. When finally combined with reliable behavioural data, this will yield superior understanding of the biological function such adapted iridescence strategies offer their hosts.

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Cognitive Neuroscience: Distinguishing Self from Other

Neurons in medial frontal cortex have been found to distinguish between whether an animal or its partner is responding on a turn-taking task, but are they really the basis of a social learning mechanism?

Stephanie Burnett and Masud Husain

Isn't it irritating when people cannot wait their turn and interrupt? The ability to 'take turns', whether during a conversation or other cooperative activity, is a fundamental requirement for successful social interactions. At just a few months of age, human infants show evidence of engaging in interactions with their caregiver, including taking their turn [1]. Social development continues through childhood and adolescence, with emerging awareness of a social concept of self as viewed by other people [2]. Such abilities are considered to be evidence for neural mechanisms that distinguish between 'self' and 'other'.

By contrast, an ever-expanding literature on 'mirror neurons' — neurons that respond *similarly* to actions of self and other — has shifted attention to brain mechanisms that do not distinguish between whether we perform an act, or someone else does. Much has been written about the possible functions of such mirror neurons [3–5], but evidence for single neurons involved in the converse function of distinguishing self from other has, until recently, been conspicuously absent [6]. A primate electrophysiology study [7] published recently in *Current Biology* provides novel evidence for a role of the medial frontal cortex in differentiating self from other's action during a turn-taking task in which it is imperative not to interrupt.

Yoshida *et al.* [7] trained two macaques to perform a rewarded task. On each trial, one animal was assigned the role of actor, and the other was an observer. Roles alternated every two trials. During each trial, the actor made a choice between a green or yellow illuminated button, the position of which could swap randomly; whereas the observer simply held down a red button for the duration of the trial. Both animals received a juice reward if the actor made the 'correct' choice, and both animals could see the other's actions. The button colour that was rewarded remained constant for several trials, but reward contingencies switched without warning every so often. So now the animal whose turn it was to act had to switch to choosing the alternative coloured button. Thus, reward expectation was constant across animals on a given trial, and the experimenters were able to identify agent-specific neural signals.

Recordings were made from medial frontal cortex during actor and observer trials. In line with a recent human electrophysiology study [8], mirror neurons were observed that fired similarly to a green or yellow choice made by either animal. But, in addition, the authors observed 'partner neurons'. These fired selectively to a choice made by the partner and, in the main, remained unmoved during the choices of self. The authors argue that partner neurons provide a neural substrate for self–other differentiation which enables social learning in the task.

Recordings were made in two adjacent sites, the pre-supplementary motor area (pre-SMA) and the cingulate sulcus, with partner neurons being encountered more frequently in the pre-SMA. Yoshida *et al.* [7] speculate that these neurons might play a critical role in social learning. Indeed, studies of Theory of Mind — the attribution to others of mental states that account for their behavior, for example, 'my partner believes the green button will be rewarded' — have implicated medial frontal regions, together with the temporoparietal junction, in this function in humans [9–11]. The authors suggest that connections between multisensory superior temporal sulcus (STS) and pre-SMA might form a brain network involved in assigning agency.

Focal damage to the STS in humans can lead to unusual syndromes, for example loss of possession of one's own arm [12], perhaps consistent with a role for agency. However, the medial frontal areas that are considered to be important for Theory of Mind in humans are located far more anteriorly (rostral) to the pre-SMA [9]. Furthermore, their precise contribution is unclear as bilateral lesions to them can leave Theory of Mind intact [13].

Nevertheless, the proposed function of partner neurons in assigning agency to other versus self would be a necessary first step in the assignment of discrete mental states to other — wherever that might be computed in the brain. In this way they might be considered precursors to a social agency or social learning system. But is self–other differentiation, or indeed 'social learning', the best way to consider such activity? The precise role of the pre-SMA is far from clear and it has been implicated in several different types of function [14–18].

Converging lines of evidence from single unit recordings in macaques, as well as human functional neuroimaging and lesion studies, has led to the proposal that the pre-SMA represents complex condition–action associations [18]. These contain links between stimulus and response which can be described as multiple, conditional or poorly specified, and of course may depend upon previous experiences and their outcomes — positive or negative.